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BRIEF REVIEW

The Value of Enrichment to Reintroduction Success

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Reintroduction attempts have faced low, albeit improving, success rates, especially for threatened and endangered species reintroduced from captivity to the wild. This is not only a concern for conservation, as the low success of reintroduction also implies an animal welfare issue for the individuals concerned. Success rates are particularly low for species that live in complex social structures, require greater training during development, and exhibit higher levels of intelligence. Aside from mitigating the original cause of a species extirpation from an area, behavior factors arguably represent the most important aspect influencing an animal's survival following reintroduction. Indeed, we previously recommended using behavioral indicators for determining relative reintroduction success, especially as practitioners develop and compare protocols or if survivorship is difficult to gauge. Strategic enrichment programs targeted toward developing specific skills important for survival in the wild promise to improve reintroduction success by providing individuals with opportunities to develop and improve behavioral skills, such as avoiding predation, foraging (especially for predators and primates), interacting in social groups, courtship and mating, habitat selection, and learning movement and migration routes. Enrichment also improves the physical condition of most individuals, which should also increase reintroduction success. Last but not least, such programs offer the prospect of improved animal welfare both pre- and post-release. We explore how behavioral enrichment has influenced reintroduction success and welfare in a variety of different species. Zoo Biol. 32:332–341, 2013. © 2013 Wiley Periodicals Inc.

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INTRODUCTION

Environmental enrichment is an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological wellbeing [Shepherdson, 1998:1]. Enrichment is also emerging as an increasingly important method for improving captive breeding and release programs. To succeed, reintroduction programs require high captive breeding success and low captive mortality rates to allow them to provide animals for release that will survive and breed in the wild. Released individuals require a wide range of behavioral skills and cognitive abilities that depend, in part, on the environments in which they are reared and their immediate pre-release experience [Shepherdson, 1994; Miller et al., 1998; Rabin, 2003]. Therefore, for the purposes of this paper we define environmental enrichment as changes in management strategies directed at improving the wellbeing of animals. Most commonly environmental enrichment focuses on animals destined to live out their lives in captivity. However, we believe enrichment also has much to offer reintroduction programs by increasing the chances of individuals breeding, surviving, and reproducing both prior to and following reintroduction into the wild. As such, our definition extends somewhat beyond what most captive animal managers would include within more traditional definitions of the phrase environmental enrichment.

Preparing animals for survival in the wild may appear to contradict more traditional notions of enrichment because it sometimes requires subjecting them to unpleasant or

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"stressful" stimuli that may seem to conflict with good welfare. We have two responses to this apparent paradox. First, nature contains many stresses that hone animals' adaptive behavioral responses. Stress fundamentally differs from distress. Distress results from a novel stimulus for which the animal has no adaptive response. For example, chronic distress of caged animals may result in abnormal behaviors (e.g., pacing in a cage, pulling out fur, failing to reproduce) because animals lack the adaptive behavioral outlet to control their situation. On the other hand, periodic bouts with natural stresses benefit animals by improving their behavioral skills. Indeed, animals may require natural stresses for normal psychological and behavioral development [Moodie and Chamove, 1990; Shepherdson, 1994]. Meehan and Mench [2007] make a compelling argument that captive animals lack "challenge" compared to their wild counterparts. Challenge can take many forms and needs to relate to the natural biology of a species, but it is consistent with the idea that not all experiences in captivity need to be positive, at least in the first instance. Our second response is that animal welfare should not apply only to animals in our care; if we truly care for the animals in our programs, then we must think about the quality of their post-release lives. Animals released without the tools to survive in the wild will unlikely live in a state of good wellbeing, at least initially [Swaisgood, 2010]. Snyder [1977] went as far as to suggest that survival of captive reared animals in the wild is the standard by which captive environments should be judged.

Historically, most reintroductions have failed [Griffith et al., 1989; Kleiman, 1989; Beck et al., 1994; Wolf et al., 1996; Griffin et al., 2000; Shier and Owings, 2006]. Other reintroductions are not as effective or efficient as they could be [Backhouse et al., 1994; Miller et al., 1996; Shier and Owings, 2006]. In recent years, it appears that success rates may be improving [Soorae, 2008, 2010, 2011], although little systematic analysis has occurred and practitioners likely report failures only rarely. As the biodiversity crisis continues and populations of many species continue to decline, restoration becomes an increasingly important conservation tool and reintroductions will likely grow in importance. Thus, we need to work to improve reintroduction success rates. Providing strategic enrichment programs targeted toward developing specific skills important for survival in the wild to individuals selected for reintroduction, especially for animals being reintroduced from captivity to the wild, promises to increase survival by improving physical conditioning, behavioral expression, and other skills [Miller et al., 1990a,b; Shepherdson, 1994; Biggins et al., 1999; McLean et al., 2000; Banks et al., 2002; McPhee and Silverman, 2004; Watters and Meehan, 2007; Ncube and Ndagurwa, 2010]. Enrichment may also increase reproduction in captivity, often an essential pre-requisite to reintroduction programs using animals from captivity [Carlstead and Shepherdson, 1994; Martin and Shepherdson, 2012].

In this paper, we discuss how strategic enrichment programs can influence the success of reintroductions, or more generally translocations. We define translocations as moving organisms from one area to another. We emphasize returning species to areas where their populations have been extirpated (reintroduction) because releasing animals to augment an existing population (restocking) and releasing animals outside their historical range (introduction) are generally inadvisable [IUCN, 1987], although they can be useful under special circumstances [e.g., Gerrodette and Gilmartin, 1990].

We have worked within or consulted on several reintroduction programs or proposed programs, including black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanni*) in the western U.S. (we used neutered Siberian polecats as surrogates to test reintroduction techniques that we could apply to black-footed ferrets), eastern barred bandicoots (*Perameles gunnii*) in Victoria, Australia, European mink (*M. lutreola*) in Estonia, giant pandas (*Airulopoda melanoleuca*) in China, Turks and Caicos rock iguanas (*Cyclura carinata*) in the Turks and Caicos Islands, Bali mynahs (*Leucopsar rothschildi*) in Indonesia, and bison (*Bison bison*), gray wolf (*Canis lupus*), California Condor (*Gymnogyps californianus*), pygmy rabbit (*Brachylagus idahoensis*), Oregon spotted frog (*Rana pretiosa*), and Canadian lynx (*Lynx canadensis*) in the U.S. [Backhouse et al., 1994; Miller et al., 1996; Reading et al., 1999, 2010, 2011; Campbell et al., 2006; Walters et al., 2010; Martin and Shepherdson, 2012; Tidwell et al., in press]. We use these case studies and others from the literature to inform our discussion.

FACTORS INFLUENCING REINTRODUCTION SUCCESS

A wide variety of biological and socio-economic factors influence reintroduction success [Griffith et al., 1989; Kleiman, 1989; Stanley-Price, 1989; Reading et al. 1991, 1997, 2004; Miller et al., 1996, 1999; Reading and Clark, 1996]. Important biological considerations include genetics, demography, disease, habitat requirements, and behavior [Reading and Clark, 1996; Miller et al., 1999]. Understanding these considerations can increase success rates and provide baseline data against which to compare the results of reintroduction programs [Miller et al., 1999; Stoinski et al., 2003]. Important behavioral traits that may influence reintroduction success include locomotion skills (e.g., moving in complex environments, constructing home sites like dens and nests, and movement patterns), predator avoidance (recognition and evasion), foraging (including finding, identifying, acquiring, and handling food), interacting in social groups (including courtship, mating, and raising and training young), habitat selection, and avoiding conflicts with humans [Derrickson and Snyder, 1992; Beldon and McCown, 1996; Miller et al., 1996, 1998; Snyder et al., 1996; Griffin et al., 2000; McPhee, 2003; Stoinski et al., 2003; de Azevedo and Young, 2006a,b; Alberts, 2007; Utt et al., 2008]. Reintroducing captive-born animals with poor behavioral skills often results in high mortality rates [Griffin et al., 2000; Stoinski et al., 2003; McPhee and Silverman, 2004; Shier and Owings, 2006]. Mitigating these problems during a reintroduction of captive-raised black-footed ferrets was time-consuming and expensive [see Miller et al., 1996; Biggins et al., 1999].

Because of high variance and small sample sizes, assessing reintroduction techniques by survival may prove statistically challenging. To survive, however, reintroduced individuals must perform behaviors efficiently in a variety of situations and in the context of other simultaneous behaviors [Stoinski et al., 2003; McPhee and Silverman, 2004; Watters and Meehan, 2007]. As such, we echo the suggestion of other authors to use behavior as a measure of reintroduction success [Kleiman et al., 1990, 1994; Miller et al., 1996, 1998; Stoinski et al., 2003], and Box [1991] suggests selecting individuals for release based on how well they perform important behaviors. Knowing how an animal forages, acquires food, avoids predation, reproduces, parents, communicates, selects habitat, locomotes, and moves daily and seasonally, as well as its imprinting periods, social organization, and territoriality, can all affect the selection of individuals for release, timing and method of release, and choice of release sites.

Wild Versus Captive Source Animals

Reintroductions that use wild-born animals generally fare better than programs that use captive-born animals [Griffith et al., 1989; Brightsmith et al., 2005; Shier and Owings, 2006; but see Wolf et al., 1996]. As such, reintroduction programs should rely on captive source populations only as a last resort [Miller et al., 1999]. Despite efforts to avoid it, artificial selection in captive environments can erode the genetic basis for morphological, physiological, and behavioral traits [Miller et al., 1999; McPhee, 2003; McPhee and Silverman, 2004; Kraaijeveld-Smit et al., 2006; Shier and Owings, 2006; Fraser, 2008]. As a result, captive-born individuals may not perform the correct behavior in a given situation or may not perform the behavior well enough to survive in the wild [Miller et al., 1999; McPhee, 2003]. Captive animals tend to habituate to their human caretakers, which often leads to increased human–wildlife conflicts and reduced survival post-release [Beldon and McCown, 1996]. As such, enrichment programs that help develop proper human avoidance skills can prove crucial to reintroduction success. The captive environment influences different species and even different individuals within a species to varying degrees [McPhee, 2003; Watters and Meehan, 2007]. However, in general, more time and generations in captivity increases the degeneration of behavior skills, thereby reducing survivorship following reintroduction [Frankham, 1995; Snyder et al., 1996; McPhee, 2003; McPhee and Silverman, 2004; Kraaijeveld-Smit et al., 2006; Shier and Owings, 2006]. Learned behaviors often degrade more rapidly than genetic diversity in captive environments [May, 1991, but see also Alberts, 2007]. In some cases, no amount of pre-release enrichment, other preparation, and post-release training may produce survival rates for captive-reared animals that approximate survival rates of wild-born individuals during dispersal [Griffin et al., 2000; Stoinski and Beck, 2004]. Using enrichment in captivity to develop the adequate expression of important behaviors requires (1) an appropriate environment for learning, (2) sufficient opportunities to express the behaviors, (3) the correct social setting (e.g., presence of a skilled parent or other relative, correct social group), and (4) understanding the role developmental factors may play in the timing of stimuli, as in the case of imprinting where the proper stimulus must occur at the right time in development [Gossow, 1970; Miller et al., 1999; Griffin et al., 2000; Stoinski and Beck, 2004; Watters and Meehan, 2007].

Experimental releases that compared captive to wild born individuals of the same species found that captive born animals displayed different behaviors and poorer survival than wild born individuals [Schadweiler and Tester, 1972; Cade et al., 1989; Griffith et al., 1989; Beck et al., 1991, 1994; Biggins et al., 1991; Wiley et al., 1992; Beldon and McCown, 1996; Miller et al., 1996; McPhee, 2003; McPhee and Silverman, 2004; Mathews et al., 2005; Kraaijeveld-Smit et al., 2006; Shier and Owings, 2006; Roe et al., 2010]. Captive born pumas (*Puma concolor*) in Florida demonstrated less fear of humans and a greater likelihood of puma-human and puma-livestock conflicts than wild born animals [Beldon and McCown, 1996]. Captive born northern water snakes (*Nerodia sipedon sipedon*) exhibited reduced surface movement and abnormal habitat use, resulting in higher mortality rates than wild-born, translocated snakes [Roe et al., 2010]. Finally, McPhee [2003] found that the more generations that she maintained old field mice (*Peromyscus polionatus subgriseus*) in captivity, the greater the loss of anti-predator behaviors and the higher the variance in those behaviors.

THE VALUE OF ENRICHMENT TO REINTRODUCTION

Enrichment promises to improve survival rates of individuals reintroduced from captivity to the wild and, in some cases, even for animals translocated from wild source populations. Yet, enrichment can prove difficult and costly. As such, we encourage rigorous testing of enrichment protocols to ensure that they aid post-release survival. Few reintroductions conduct formal, rigorous evaluations of release methods or adequately monitor the fate of reintroduced individuals, despite the importance of doing so to improve future success rates [Kleiman et al., 1994, 2000; Miller et al., 1996, 1998; Reading et al., 1999]. Such research and monitoring not only promises to continually improve reintroduction programs, but should also help increase efficacy by eliminating the need for expensive, but ineffective protocols.

We believe that enrichment could improve several important behavioral skills of animals prior to reintroduction, help in selecting individuals with a higher probability of surviving post-release, and increase individuals' physical fitness. A conceptually simple, but often logistically difficult and expensive, form of enrichment entails providing a captive environment that mimics release sites as closely as possible [Roe et al., 2010]. Such captive environments may help increase locomotor and foraging skills, social skills, physical fitness, and the chances that animals will not disperse following reintroduction [Berg, 1982; Jacuart et al., 1986; Stanley-Price, 1989; Bangs and Fritts, 1996; Linnell et al., 1997]. Many reintroduction programs build holding pens on release sites or hold animals in situations that closely mimic release sites to facilitate the transition from captivity to the wild or from one wild site to another [Miller et al., 1996; Biggins et al., 1999; Banks et al., 2002; Boyd and Bandi, 2002; Shier and Owings, 2006; Walters et al., 2010]. For example, in the case of black-footed ferret experiments, we hauled soil into large warehouses to create enclosed prairie dog colonies [Miller et al., 1996]. Similarly, Estonian conservationists built holding pens for European mink on streams in the wild prior to releasing animals on an off-shore island [Macdonald et al., 2002]. Lastly, adult Columbia Basin pygmy rabbits reared in captivity and released into a protected 2.5 ha breeding exclosure at the release site experienced lower rates of neonatal mortality and higher post release survival [Shepherdson and Becker, Personal Observation.] and providing soil resulted in lower fecal corticosteroid levels [Scarlata et al., in preparation].

Providing enrichment early in an individual's life promises to increase success rates, as most species learn better earlier in life and some species have sensitive periods during which they imprint (on food, etc.) [Miller et al., 1996; Griffin et al., 2000; Stoinski et al., 2003]. For example, all black-footed ferrets imprint on preferred food items between 2 and 3 months of age, a time at which captive animals destined for reintroduction should receive prairie dogs (*Cynomys* spp.) as food [Vargas, 1994]. The olfactory imprinting period for ferrets during this period leads to an immediate preference for prairie dogs when they later begin to hunt. Apfelbach [1978, 1986] first found this critical period for olfactory imprinting in closely related domestic ferrets (*Mustela putorius furo*). He further correlated olfactory imprinting with neural development. Similarly, parent raised Condors display less solitary feeding than puppet reared birds following release [Utt et al., 2008]. Animals who miss critical experiences during their imprinting period may still learn to perform tasks, but would likely do so less efficiently than animals who received the correct experiences during the imprinting period. Golden-lion tamarins (*Leontropithecus rosalia*) allowed to free-range in zoos prior to release performed no better than animals with no free-ranging experience, possibly because the enrichment occurred too late in the animals' lives [Stoinski et al., 2003; Stoinski and Beck, 2004]. The early developmental environment may also influence the ability of animals to learn and respond to stressful situations later in life. A lack of complexity in the developmental environment of an individual negatively impacts its neural development, with wide ranging implications for adult behavior and survival. For example, a classic study by Pfaffenberger et al. [1976] demonstrated a difference between dogs reared in complex environments in the country compared to dogs raised in more sterile city dwellings.

Environmental enrichment may provide a wide variety of benefits to individuals destined for reintroduction. Here we discuss just a few ways in which environmental enrichment could help improve reintroduction success rates.

Locomotion

Most species probably do not require much training in locomotion. However, arboreal and semi-fossorial species may not receive the opportunities to sufficiently develop the skills needed to move rapidly and efficiency through their environments and to find their way around a complex three-dimensional space. Enrichment training for primates has provided animals with the opportunity to move through more complex arboreal habitats. For example, the golden-lion tamarins reintroduction program permits limited free-ranging opportunities in zoos for animals destined for reintroduction [Kleiman et al., 1990; Stoinski et al., 2003; Stoinski and Beck, 2004]. However, as we discuss briefly above, recent research questions the success of this program for adult animals, suggesting the importance of age-specific enrichment [Stoinski et al., 2003; Stoinski and Beck, 2004]. Nevertheless, well-developed enrichment programs may support the appropriate development of locomotion skills in captive orangutans (*Pongo* spp.), gibbons, and other primates destined for release back into the wild [Cheyne et al., 2008; Thorpe et al., 2009]. Similarly, providing opportunities for semi-fossorial animals may improve survivorship. Black-footed ferrets and Siberian polecats raised in semi-natural conditions dispersed less and spent less time above ground (and subject to predation) than did pen raised animals [Miller et al., 1996; Biggins et al., 1999]. Alternatively, some newly released animals move too little because of their unfamiliarity with escape routes and safe, rich patches of food, thus generating high concentrations of wastes with odors that attract predators [Banks et al., 2002]. Providing acclimation pens on reintroduction sites may mitigate this problem.

Predator Avoidance

Closely linked to locomotion, reintroduced animals obviously must avoid predation to survive long enough to reproduce for programs to succeed. For many species, predation represents the most immediate threat to the survival of released animals, and indeed a substantial body of literature focuses on the importance of predator avoidance to reintroduction success [Miller et al., 1990b; Griffin et al., 2000; McLean et al., 2000; Banks et al., 2002; McPhee, 2003; Rabin, 2003; McPhee and Silverman, 2004; de Azevedo and Young, 2006a,b; Kraaijeveld-Smit et al., 2006; Shier and Owings, 2006; Alberts, 2007]. Predation especially threatens captive-reared animals or animals released into areas with novel predators, as reintroduced animals may not recognize predators or react appropriately [Miller et al., 1990b; Maloney and McLean, 1995; McLean et al., 2000; Griffin et al., 2001; McPhee, 2003; de Azevedo and Young, 2006a; Shier and Owings, 2006].

The threat of predation has prompted many reintroduction practitioners to use enrichment to improve predator avoidance skills in individuals prior to release [Miller et al., 1990b, 1994, 1996; Maloney and McLean, 1995; Biggins et al., 1999; Griffin et al., 2000, 2001; de Azevedo and Young, 2006a,b; Shier and Owings, 2006]. This usually entails presenting models of predators and delivering an aversive experience to individuals prior to release. The experience must be aversive because avoiding predators differs from searching for food (positive reward). Responses motivated by positive and negative stimuli occur in different parts of the brain [Miller et al., 1996].

We used predator models to assess the innate and learned components of predator avoidance in Siberian polecats (as a surrogate for black-footed ferrets) [Miller et al., 1990b]. We exposed naïve polecats to a predator model at 2–4 months of age (at 2 months of age black-footed ferrets first appear above ground and they disperse at 4 months). At 3 and 4 months of age, naïve polecats showed an innate response to the model, and they improved that response after an aversive experience [Miller et al., 1990b]. Presenting Greater Rheas (*Rhea americana*) and several species of wallabies with model predators associated with chases by people or dogs or captures by people led to increased predator avoidance [McLean et al., 2000; Griffin et al., 2001; de Azevedo and Young, 2006a,b].

Predator avoidance training tends to require only a few trials; indeed more trials may habituate captive animals to the predator [Griffin et al., 2000; Shier and Owings, 2006]. As such, captive animals likely would require only limited predator avoidance enrichment. Most programs conduct this training only prior to release, but it may make sense to conduct such training on an on-going basis periodically for captive populations associated with reintroduction programs.

For many species, humans represent the most important potential predator to avoid, especially for species highly prized by poachers, such as rhinoceros and parrots [Matipano, 2004; Brightsmith et al., 2005; Hutchins and Kreger, 2006; McDougal et al., 2006; Alberts, 2007]. This can present a significant problem for animals habituated to people during captive breeding [Matipano, 2004]. Some programs, such as black-footed ferret and California condor reintroductions attempt to rear animals destined for release with the least human interaction possible to avoid habituation and to ensure that any necessary human interactions are aversive in nature [Miller et al., 1996; Biggins et al., 1999; Snyder and Snyder, 2000]. Ethical issues may arise in training predator avoidance since exposure to predators is most likely stressful; however, at least one study suggested that when provided in appropriate context such brief threatening events provide benefits [Moodie and Chamove, 1990].

Foraging Skills

Reintroduced animals must forage efficiently to survive. Foraging includes identifying and finding high quality foods, food acquisition (e.g., killing prey, climbing trees to reach fruit), and food handling/processing time (e.g., shelling nuts, removing feathers or hair) [Young, 1997; Mathews et al., 2005; Cheyne et al., 2008]. Many species rely on significant training from parents or helpers prior to becoming proficient [Ncube and Ndagurwa, 2010]. For predators, finding, stalking, and killing prey requires a substantial amount of skill that captive animals rarely acquire [Miller et al., 1990a, 1999; Young, 1997; Ncube and Ndagurwa, 2010]. Two captive-raised fishers (*Martes pennanti*) that killed prey on their first exposure in captivity, later starved to death after release into the wild, presumably because could not locate prey [Kelly, 1977]. Learning how to search for food from a parent may have been the missing ingredient.

Enrichment programs can facilitate learning and skill acquisition in all of these areas [Biggins et al., 1999; Ncube and Ndagurwa, 2010]. For example, black-footed ferrets raised in pens with live prairie dogs displayed higher predatory proficiency than cage-reared ferrets [Vargas, 1994; Biggins et al., 1999]. Alternatively, as with locomotion, golden-lion tamarins provided with enrichment did not demonstrate better foraging abilities than animals without enrichment, possibly because the enrichment occurred too late in the animals' lives [Stoinski et al., 2003; Stoinski and Beck, 2004]. In some cases, simply providing animals with food they will encounter following release will help develop food recognition and foraging skills [Young, 1997]. In other cases, programs might use conspecifics with already acquired skills to help train individuals without those skills. More generally, enrichment devices that present animals with foraging challenges, such as puzzle foraging devices used for captive orangutans, build more general thinking and dexterity skills. For predators, ethical issues may preclude providing live prey in some circumstances, yet may be crucial as most animals become more proficient with more experience [Miller et al., 1996; Young, 1997]. We found that naïve Siberian polecats took about 20 min to kill a live prairie dog on their first attempt, but by their third experience they took less than 5 min to subdue their prey. Improving prey acquisition efficiency before release is critical to survival post-release [Miller et al., 1990a]. Periodically fasting animals that typically do not feed on a regular basis also better prepares them for reintroduction [Young, 1997].

Social Interactions

Sociality varies among wildlife species. Some species live in groups while others lead more solitary lives, but primarily solitary animals still communicate their presence, level of dominance, sex, and state of sexual receptivity to neighbors. Strategic enrichment programs may require providing opportunities for antagonistic interactions among captive animals to hone skills if such interactions will likely occur in the wild (e.g., over clumped food resources or access to mates) [Watters and Meehan, 2007].

Group living species require greater social integration and training prior to release. Removing colonial animals from the wild can disrupt social bonds and lead to deterioration or even loss of social skills needed for complex interactions. For example, gibbons learn calls from their parents and populations likely have different dialects, complicating possible reintroductions [Cheyne et al., 2007]. Play back experiments with gibbons in zoos suggest that auditory enrichment may effectively replicate aspects of wild vocal interactions [Shepherdson, 1988].

Before mating, many animals engage in courtship behavior, which is a form of communication important to mate recognition. Some species exhibit quite complex communication patterns, and an unfamiliar action, or the incorrect response to an action, can terminate the courting process. In some species, females must receive the correct male courtship behavior to heighten receptivity [Crews, 1975; Silver, 1978; Welbergen et al., 1987]. Black-footed ferrets displayed a pattern of female solicitation followed by resistance, perhaps as a way of testing male tenacity and maturity [Miller et al., 1996]. Nearly all carnivores show some correlation between rank and copulatory success and lengthy courtship interactions, such as that for black-footed ferrets, may test male dominance [Alcock, 1984]. Such female selection may assure that a dominant male sires her offspring [Miller et al., 1996]. For example, female mate selection is important for endangered Columbia Basin Pygmy rabbits [Martin, 2009], and probably a wide range of other species as well. Thus, enrichment programs may need to provide animals with the opportunity to hone courtship and mating behavioral skills. In some cases, this may require competition for mates and opportunities for female mate choice.

Reintroductions of colonial species, such as prairie dogs, may require translocating entire family or social groups to improve survivorship. For example, black-tailed prairie dogs (*Cynomys ludovicianus*), reintroduced in family groups enjoyed higher survivorship and reproductive success than individuals reintroduced without regard to family group [Shier, 2004]. Mixing members of different social groups may lead to conflict, especially during the critical, early post-release period. Similarly, bison live in smaller family groups within larger herds [Berger and Cunningham, 1994; Lott, 2002]. Reintroducing entire family groups maintains social structures, thereby decreasing conflict and maintaining better opportunities for learning and transmitting information [Boyd and Bandi, 2002; Ncube and Ndagurwa, 2010]. Enrichment programs often strive to maintain social groups, but those social groups should remain intact during reintroduction programs whenever possible [Boyd and Bandi, 2002]. Reintroducing naïve animals with more experienced conspecifics may also improve survivorship [Stoinski et al., 2003].

Physical Fitness

Providing enrichment improves the physical fitness of animals prior to release [Biggins et al., 1999; Mathews et al., 2005]. Most animals from captive environments receive insufficient exercise and opportunities to develop the level of fitness they will require subsequent to release. For example, after we released captive bison into a ranched herd in Colorado, the captive-born and dominant ranch-born males almost immediately began to fight. The ranch-born male easily dominated the captive-born male for weeks until the larger captive-born male's fitness improved to the point that he ejected the ranch-born male from the herd. Most mortalities among reintroduced animals occur during the period immediately after release, when animals are least fit and simultaneously face challenges of avoiding predation and learning about their new environment [Miller et al., 1990b]. Once released, captive-born animals often face exposure to microorganisms and parasites for the first time, which can further weaken their condition [Biggins et al., 1999]. Some authors recommend assessing the physical fitness and temperaments of individuals prior to selecting animals for release and either selecting individuals that practitioners believe display behavioral traits most similar to wild conspecifics [Bremmer-Harrison et al., 2004; McDougal et al., 2006] or selecting individuals with a broad range of behavioral traits and letting selection act on those [Watters and Meehan, 2007]. Although Griffith et al. [1989] reported no correlation between an animal's physical condition of and its post-release survival, we advocate releasing animals in good physical condition and good health before release. A good enrichment program can help develop and maintain physical conditioning.

Selecting Individuals for Release

Knowledge of hunting, killing, predator avoidance, imprinting, reproduction, locomotion, daily and seasonal movements, timing of reintroduction, method of release, and site fidelity all affect selection of individual animals for release [Miller et al., 1999]. Providing enrichment to animals in captivity and monitoring their responses can help identify individuals with a higher probability of surviving following reintroduction. Along these lines standardized behavior tests allow us to measure temperament. The important role that temperament plays in the welfare of zoo animals is just beginning to be appreciated [Carlstead et al., 1992; Powell and Gartner, 2011; Watters and Powell, 2012; Shepherdson et al., in press]. Temperament likely represents an important factor for selecting individuals for release both in terms of survival and welfare. For example, reintroductions of swift foxes (*Vulpes velox*) found that bolder individuals from captivity suffered higher mortality rates following release [Bremmer-Harrison et al., 2004]. Bolder animals probably showed insufficient wariness of predators such as coyotes. Practitioners could use enrichment to help assess such "personality traits" or temperaments in captive animals and thereby avoid releasing animals that scored higher on traits or temperaments linked to risky behaviors or behavioral responses to novel stimuli [Bremmer-Harrison et al., 2004; Mathews et al., 2005; McDougal et al., 2006; de Azevedo and Young, 2006a,b; Watters and Meehan, 2007]. That said, reintroduction programs should strive to maximize genetic diversity among release animals [Kleiman, 1989; Reading and Clark, 1996; Miller et al., 1999]. Greater genetic diversity reduces the chances for founder effects and inbreeding depression, which can compromise small populations struggling to become established. Greater diversity may also enable the population to better adapt to its habitat.

As mentioned above, wild-born animals are preferable to captive-born animals for translocations [Griffith et al., 1989], and we recommend releasing captive animals only when there are no other alternatives. Captive environments may erode the genetic basis for important morphological, physiological, and behavioral traits via artificial selection [McPhee, 2003, 2004], especially in the absence of a well-planned enrichment program. The more generations a population spends in captivity without an enrichment program, the greater the deterioration of survival skills [McPhee, 2003]. Young animals often display greater behavioral plasticity than adults, so enrichment programs can more easily influence them. Behavioral studies of captive and wild populations may help practitioners select captive-bred individuals with the best chances for survival following release [McPhee and Silverman, 2004].

ASSESSING THE EFFECTIVENESS OF ENRICHMENT TECHNIQUES

We believe that appropriately designed enrichment programs could improve reintroduction success rates, possibly dramatically. However, we also recognize that few studies have adequately evaluated the contribution of enrichment programs to reintroduction success. We recommend that reintroduction practitioners rigorously test the impacts of enrichment programs on success rates and on the efficacy of such programs. Here we offer some steps forward toward this goal.

Where possible, we recommend running reintroduction programs as experiments, especially in the early stages. By controlling as many variables as possible, we will better understand the value of enrichment programs to reintroduction success. Given the added time, effort, and expense of strategic enrichment programs, an obvious first step would entail comparing animals released with and without exposure to enrichment. Ideally, such studies would compare vital (survival and reproductive) rates, but given the difficulty and often long periods required to do so, we recommend also examining behavioral variables such as activity patterns, dispersal distances from the reintroduction site, and social interactions as well. Often behavioral variables will provide earlier indications of potentially important differences. For example, animals dispersing further from the release site and remaining active outside of time periods typical for the species will likely face greater predation pressure over time. Research should begin with enrichment programs targeting key behaviors known to influence vital rates most strongly and then move to other behaviors or to refining targeted behaviors. Some programs may begin with more comprehensive enrichment programs that address several behaviors (e.g., foraging skills and predator avoidance). If researchers find that the program that addresses several behaviors influences reintroduction success, subsequent studies may address each of those variables separately. For example, experimentation with pre-release enrichment greatly improved black-footed ferret reintroduction success rates over time as discussed above [Miller et al., 1996; Biggins et al., 1999]. However, even findings of no significance differences (as with the golden lion tamarin example discussed above) represent important findings as they increase efficacy by eliminating the need for costly pre-release conditioning.

Experiments can use surrogates for rare species. For example, we used Siberian polecats for experiments around captive breeding and reintroduction [Miller et al., 1996]. The Arabian oryx (*Oryx leucoryx*) reintroduction project used the fringe-eared oryx (*Oryx gazelle callotis*) as a surrogate and the California condor project used Andean condors (*Vultur gryphus*) to test reintroduction techniques.

Reintroduction programs should strive to retain strong science components until results permit practitioners to refine protocols, including strategic enrichment programs. This often requires careful attention to public relations and the political atmosphere of the program, especially for high profile programs. For example, issues of program control interfered with initial attempts to incorporate a strategic enrichment program into the black-footed ferret reintroduction program [Miller et al., 1996]. Similarly, the state of Colorado abandoned early plans to compare different release protocols for a Canada lynx reintroduction into that state in the face of heavy public pressure [CDW, 2000]. High mortality rates plagued early releases that failed to follow the initial experimental design due to logistical problems [CDW, 2000; Devineu et al., 2011]. Despite the program's success in establishing a population of lynx, we learned little about the value of enrichment to released animals.

CONCLUSIONS

The high incidence of reintroduction failure implies a significant compromise of animal welfare for the individuals involved. We join others [e.g., Fraser, 2010] in arguing that it is no longer ethically acceptable to concern ourselves with the welfare of populations at the expense of individual welfare. Enrichment promises to improve the welfare of animals involved in reintroduction programs while simultaneously increasing success rates by helping to address many of the behavioral physical fitness considerations that impact many of these programs. As conservation programs increasingly use reintroduction to help recover species, improving success rates has never been more important. Aside from mitigating the original cause of a species extirpation from an area, behavioral considerations may represent the most critical factors affecting post-release survival. Thus, in programs relying on captive animals, having an adequate enrichment program may mean the difference between success and failure. We, like others, recommend using behavioral indicators to determine reintroduction success, particularly during the early stages. Appropriately designed enrichment can improve reintroduction success by providing more individuals for release and by providing released animals with opportunities to develop and improve behavioral skills, such as avoiding predation, foraging (especially for predators and primates), interacting in social groups, courtship and mating, habitat selection, physical conditioning, and learning movement and migration routes. The benefits of incorporating enrichment into reintroduction programs go well beyond simply learning survival behaviors since animals that are less stressed, healthier, given appropriate choices such as with whom they will mate, and allowed to fully develop their cognitive abilities will more likely reproduce, display normal behaviors, and adapt to new environments following release. As species increasingly face extinction, reintroduction programs grow in importance and enrichment programs promise to improve the success rates of those programs.

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